ON EVOLUTION OF ENDOPARASITISM: THE BIOLOGY OF SOME GENERA OF ROGADINAE (BRACONIDAE)

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INTRODUCTION

Both ectoparasitism and endoparasitism are found in several families of parasitic Hymenoptera (parasitoids) and, since the former is generally accepted as being the more primitive, it is evident that there have been many independent evolutions of endoparasitism from different ectoparasitic ancestral stocks. One group in which this has occurred is the braconid subfamily Rogadinae (*sensu* Achterberg 1976), in which elements of the extant tribes Exothecini (ectoparasitic) and Rogadini (endoparasitic) are clearly closely related. I have investigated the biology of British species of some of the genera in these two tribes, considering particularly host range, the biology of the hosts, the host stages attacked, the use and effects of parasitoid venom, and egg placement. From this it has been possible to trace developments in the ectoparasitic habit, as efficient exploitations of given host life-histories, to the point at which it becomes so specialized and refined that it differs from the most primitive condition of endoparasitism I have seen in the Rogadini only in the relatively minor detail of egg placement on different sides of the host's integument.

The meaning of host range. Most parasitoids are not absolutely specific to single host species but instead tend to attack a group of hosts which usually bear some relation, either ecological or phylogenetic, to one another. The "host range" (or 'usual hosts") of a given parasitoid is a key feature of its biology, although in practice it is a nebulous term difficult to define with any precision. This is because some host species may be attacked less avidly, or with less success, than others, and furthermore it is known that such factors can vary from one population of a parasitoid species to another: indeed, some plasticity in behavior and variability in success have presumably been prerequisites in the evolution of host specializations at all. However, it is useful to define host range in general terms as including only the species of potential hosts that the parasitoid is usually able to attack successfully, following a pattern of searching behavior enabling it to encounter them regularly. Potential hosts that are attacked only by some freak of circumstance, or which only occasionally permit the parasitoid's full development, would thus be excluded from a useful concept of host range, as would species of otherwise suitable hosts which the parasitoid rarely encounters. In practice host ranges can usually be understood as a balance - more or less severe, and variously biased - between host ecology and host phylogeny. Not all the elements of a host range will necessarily be present at a particular site, however, so at a local level parasitoid populations often attack only a more limited set of hosts. Also, a particular host species may not be available during the whole span of a parasitoid's period of activity, especially if, as is often the case in temperate areas, the parasitoid is plurivoltine and some or all of its hosts are univoltine.

A regular parasitoid of a given host must first search in the environment supporting the host, second be able to detect and accept the host, and third be physiologically capable of full and unimpaired development upon it. There are thus two broad aspects of host range involving potential behavioral flexibility: (a) host habitat selection, or where to search, and (b) host selection, or what to attack. Host habitat selection is one of the simplest expressions of specialization, and very many parasitoids of phytophagous hosts search exclusively either on arborescent vegetation or in the field layer. The importance of the second kind of behavioral limitation to host range, whereby certain potential host species are usually rejected although proving to be suitable on the rare occasions they are attacked, is often seen in ectoparasites, which are in general under less severe physiological pressures than typical endoparasites and therefore tend to have broader potential host compatibilities.

MATERIALS AND METHODS

As wide a range as possible of larvae Lepidoptera in general and leaf-mining insects of the Orders Lepidoptera, Hymenoptera, Coleoptera and, to a lesser extent, Diptera have been collected wild from a diverse range of the habitats available in Britain and reared in captivity, firstly to obtain host records of parasitoids in general, and secondly to obtain culture material for experimental rearings. Except that some experiments involving cultures of leaf-miners and their parasitoids were conducted in muslin sleeves on trees, all material was reared in an unheated detached wooden shed, which was situated in deep shade, painted white, and permanently ventilated by replacing the window and door with wire mesh. Under these conditions air temperatures were always within 1° C of outdoor shade, and natural conditions of humidity and light were maintained at least approximately: in all cases that could be checked, emergence dates of captive host and parasitoid species corresponded to those in the field. Wild collected larvae and experimental cultures were kept as single species in carefully counted groups (of often individually) in closed tubes or plastic boxes. All larval hosts were fed on natural foodplants: leaf-mining species unable to change leaves were mostly collected as mature (or already killed or vacated) entities and the mines were cut out and tubed, or otherwise processed, individually.

In addition to my own rearings of parasitoids, I have received much reared material from lepidopterists and other entomologists who, by screening so large a number of potential hosts, have guided me to hosts producing Rogadinae on a number of occasions. Among several entomologists, B. T. Parsons, R. A. Softly and the late W. A. Watson have been particularly generous with their time spent searching for and collecting wild host species suspected of harboring Rogadinae. All of this has helped me to at least orientate towards the ideal of sampling the natural populations of parasitoids to find out what their hosts are, rather than merely sampling host populations to see what their parasitoids are.

At least some of the experimental parasitizations were carried out under full observation for all species of Rogadinae discussed below. Reared females, mated if possible, were fed on 1:2 honey:water for at least a week before being introduced singly to single hosts in clean containers, separately both naked and in situ with foodplant. Providing they were fed adlibitum and protected from extremes of temperature, most female Rogadinae lived in captivity for about eight weeks of summer. The potential hosts offered were selected to investigate both ecological and phylogenetic aspects of host range, as well as to evaluate literature records. As far as possible the host(s) from which the species had been reared were also used, especially to investigate which host stages were acceptable and suitable for successful parasitization. Although subjective, evaluations of host acceptibility (of different instars as well as different species) were surprisingly easy to make, almost all of the very many female Rogadinae tested proving to be fairly decisive in behavior, and in close agreement if conspecific.

RESULTS

Tribe EXOTHECINI

All species of Exothecini discussed have the following features in common: (a) destructive host-feeding is apparently obligatory, though light in *Rhysipolis*, and often involves hosts too small for oviposition; (b) naked hosts, as opposed to those in situ in plant material, are consistently and completely ignored; (c) very many minutes, or even hours, are usually spent investigating a host retreat for the presence of a host, and then in trying to sting it; (d) the effects of the venoms on the hosts, as described below, are irrespective of actual oviposition; (e) in all solitary species there is an ability to use the larger hosts for female progeny; (f) egg hatch and larval development are rapid (often only 4-8 days between oviposition and cocoon formation); (g) the larvae feed entirely ectoparasitically; and (h) the winter is spent as a prepupa in the cocoon.

(Genus GNAPTODON Haliday)

Although this genus is included in the Exothecini by Shenefelt (1975), I fully concur with Achterberg (in prep.) that *Gnaptodon* should be excluded from not only the Exothecini but even the Rogadinae as a whole. *Gnaptodon* species are parasitoids of Nepticulidae (Lep.), and appear to be endoparasitic (although this is yet to be thoroughly investigated).

1. Genus **COLASTES** Haliday (= *Exothecus* Wesmael)

Colastes braconius Haliday (type-species)

In Britain a widespread, abundant and regular parasitoid of a broad range of leaf-mining insects, especially of the following groups: many Agromyzidae (Dipt.) (not intensively sampled by me), most British species of which mine plants in the field layer; *Rhynchaenus* (= *Orchestes*) *fagi* (L.) (Col.: Curculionidae) on *Fagus sylvatica*; and all adequately sampled *Phyllonorycter* (Lep.: Gracillaridae) species, arboreal and otherwise, except miners in bark or tough evergreen leaves.

Less frequent as a parasitoid of various Nepticulidae, from which group as a whole it has an abnormally male-biased sex-ratio (Shaw and Askew 1976 and unpublished); Tischeriidae (Lep.) *Tischeria ekebladella* (Bjerkander) on *Quercus robur* and *T. marginea* (Haworth) on *Rubus fruticosus*); and *Mompha raschkiella* (L.) (Lep.: Momphidae) on *Chamaenerion angustifolium*.

Rarely (once each) from Eriocraniidae (Lep.) (*Dyseriocrania subpurpurella* (Haworth) on *Q. robur*); Heliozelidae (Lep.) (*Heliozela betulae*

Stainton) on *Betula pubescens* and *Antispila* sp. on *Swida sanguinea*); leaf-mining Tenthredinidae (Hym.) (*Fenusa ulmi* Sundewall on *Ulmus* and *Heterarthrus vagans* (Fallén) on *Alnus glutinosa*); and *Rhynchaenus* species other than *fagi* [*R. avellanae* (Donovan) on *Q. robur*].

Most other groups of British leaf-miners, except for Elachistidae (Lep.), have been well sampled (see in part Askew and Shaw 1974).

It may be significant that, among the Lepidoptera, none of the leaf-mining groups of Dacnonypha or Monotrysia are important hosts, the specialization of *C. braconius* being at variance with the life-histories of these. With the proviso that I have very incomplete information on the most frequently used Diptera, the important hosts of *C. braconius* were seen to (a) complete their development and pupate in a single mine; (b) inhabit blotch mines that eventually develop some degree of depth (even if only to accommodate the host cocoon, pupa, or puparium); and (c) do not isolate the pupation chamber of *R. fagi* is a merely weakly isolated swelling in the leaf apex). Thus species which change leaves, or pupate outside the mine, or strongly isolate a small pupation chamber as a reinforced and sometimes deciduous disc or sphere, are to a greater or lesser extent unsuitable for efficient exploitation and outside the host range. *C. braconius* first emerges in April or May to have several summer generations: to a large extent different host gruops are attacked at different times of year.

C. braconius was examined experimentally as a parasitoid of both *R. fagi*, and *Phyllonorycter* species on *Q. robur* and *Betula*. The host is most often attacked as a post-feeding larva, but can be parasitized successfully also during late feeding instars, or as a prepupa if only weakly cocooned. The female parasitoid probes the mine, apparently at random at least initially, repeatedly withdrawing and reinserting the ovipositor. Dead or otherwise inactive hosts are rejected, but an active host is stung when located and the ovipositor is withdrawn: a few seconds later the mine is again penetrated and a single egg is laid in the mine, apparently placed at random, and typically well away from the host. The venom received by the host causes an immediate paralysis, from which a temporary and rather variable partial recovery is often made within a few minutes. During the post-paralysis period (up to c. 1 day) the host usually remains still, and never resumes feeding or cocoon construction, although it is in some cases capable of considerable movement if disturbed. Defecation takes place and the gut usually becomes fully vacated, but the potential for activity quickly declines until, by the time the parasitoid egg hatches, the host is usually apparently dead. The first instar parasitoid larva has well-developed antennae and travels through the mine to the immobile host, on which it feeds entirely externally throughout its development on all hosts studied. [This refutes Beirne's (1946) contention, perpetrated by various subsequent authors, that it is endoparasitic]. Cocoon formation often occurs well away from the host remains, usually at the extreme edge of the mine. Mobile hosts are attacked irrespective of whether or not they are already endoparasitized but, as subactive hosts are usually rejected, superparasitism rarely occurs.

2. Genus PHANOMERIS Foerster

Phanomeris catenator (Haliday) [= ? *dimidiatus* (Nees) = ? *abnormis* (Wesmael), type-species]

In Britain a widespread and locally abundant parasitoid of the following arboreal leaf-mining sawflies (Hym.: Tenthredinidae, Fenusini): *Parna tenella* (Klug) on *Tilia*; *Messa hortulana* (Klug) on *Populus nigra*; *M. nana* (Klug) on *Betula*; *Profenusa pygmaea* (Klug) on *Quercus*; and *Fenusa ulmi* on *Ulmus*. Like other Fenusini, the hosts feed in shallow single mines and undergo post-feeding ecdysis, usually before leaving the mine (or in *F. ulmi* often immediately afterwards), to become a non-feeding eonymph which constructs a cocoon in the soil in which pupation occurs. *P. catenator* first emerges in May and is plurivoltine. Some of its hosts (e.g., *P. tenella*) are available at only particular times of year, but it is fully synchronous with others (e.g., *P. ulmi*).

In experiments *P. catenator* consistently refused to attack *Heterarthrus aceris* (Kaltenbach) and *H. vagans* (both Hym.:Tenthredinidae, Heterarthrinae), or *Scolioneura betuleti* (Klug), *Fenusa pusilla* (Lepeletier), *F. dohrnii* (Tischbein) and *Fenella nigrita* Westwood (all Fenusini). It was investigated in culture only as a parasitoid of *F. ulmi*. Host mines nearing full growth or less than half grown are consistently rejected (except for host-feeding), as are all subactive hosts. Mines from about half grown are probed repeatedly, initially at random (mines with their hosts removed were probed for up to 10 minutes before being abandoned), when the surprisingly mobile host usually wriggles away with ease. When eventually contacted, the host is stung and paralyzed: the parasitoid withdraws its ovipositor and a few seconds later again inserts it into the mine, laying an egg usually away from the host. The host recovers from the paralysis within a few minutes and usually returns to a feeding position at the edge of the mine but, although movement of its mandibles can be seen, it does not resume feeding to any appreciable extent. It remains moderately and voluntarily mobile for up to c. 1 day, and always defecates until its gut is cleared, eventually withdrawing from the edge of the mine and becoming immobile. The newly hatched parasitoid larva is similar to that of *C. braconius* and quickly locates the moribund host. The cocoon is a tough, spindle-shaped single envelope structure spun against both surfaces of the mine, generally near but not fully at the mine boundary. Parasitized hosts in their period of renewed mobility are sometimes superparasitized but it is extremely rare for more than one cocoon to result (except in multi-host, confluenct mines). Mobile hosts harboring endoparasitic Chalcidoidea are not discriminated against and, as is also seen in the case of *C. braconius*, frequently both species develop successfully as multiparasites.

Phanomeris laevis (Thomson)

In southern and central Britain, a local but sometimes abundant parasitoid of *Heterarthrus aceris* on *Acer* in midsummer, and subsequently both *H. vagans* and *Fenusa dohrnii* on *Alnus* in their autumn. The Heterarthrinae differ from the Fenusini in their pupation habits. The similar post-feeding ecdysis to an eonymph is followed by its strong isolation in a small reinforced disc within the mine, in which pupation later occurs. In *H. aceris* the disc falls from the leaf but in *H. vagans* it does not. *P. laevis* first emerges in early June and is plurivoltine (? bivoltine), using chiefly the univoltine *H. aceris* in its first generation.

In culture this species has been investigated only as a parasitoid of *H. aceris*. The biology is essentially the same as that of *P. catenator*: the host is most suitable from about half grown and host mines are rejected as they approach full growth; hosts are stung and paralyzed at first but they recover some activity, voiding the gut within a few hours but not resuming feeding, and remaining largely quiescent until again becoming immobile after c. 1-2 days; and the parasitoid egg is laid loose in the mine often some distance from the host, which is located by the first instar larva. The cocoon is a broader, double envelope structure, often spun near the edge of the mine.

3. Genus **XENARCHA** Foerster

Xenarcha lustrator (Haliday) (type-species)

A locally common parasitoid of the leaf-mining sawfly *Fenella nigrita* in southern England, on both *Agrimonia eupatoria* and *Potentilla reptans*. *X. lustrator* first emerges in June/July and is plurivoltine (? bivoltine), being well synchronized with its host.

In culture *X. lustrator* was offered *F. nigrita* mines on both its food plants. Mines about half to three-quarters grown are accepted for oviposition, those larger than this being consistently rejected. The mine-probing and host location patterns are similar to those of *Colastes* and *Phanomeris*. The host is temporarily and only partially paralyzed when stung, and the parasitoid lays one or sometimes up to three (i.e., during a single visit but probably involving separate insertions of the ovipositor) eggs loose in the mine. The initial paralyzing effect of the venom is short-lived and the host resumes feeding within c. 5 minutes, somewhat enlarging its mine during the following 6 - 12 hours before withdrawing towards the center of the mine where it becomes quiescent, though clearing the gut by defecation and being capable of movement if disturbed for a further day or two. The egg(s) of *X. lustrator* are somewhat sticky and tend to collect on the host as it contacts them during its period of temporarily recovered activity, so that the egg(s) are usually found on the host by the time it has again become inactive. (This tendency, certainly strong in both species of *Xenarcha*, was noticed on a reduced scale in *Phanomeris*, but seemed to be very slight or absent in *Colastes*. This probably reflects the relative activities of the hosts stung by these parasitoids). The egg(s) sometimes hatch before the inactive host is actually dead. The cocoon is a stout, slightly curved, bluntly spindle-shaped structure spun near the edge of the mine. Irrespective of the number of eggs laid, only one cocoon resulted from each *Fenella* mine: an attempt was made to see if *Metallus* species, also on low-growing Rosaceae but larger than *Fenella*, would be attacked and perhaps permit gregarious development but, although one larva of *M. gei* Brischke in *Geum urbanum* was stung and suffered the same pattern of vacillating activity, no eggs were laid.

Xenarcha, sp. indet.

An extremely local parasitoid of *Fenusa pusilla* on *Betula* and *F. dohrnii* on *Alnus glutinosa*, found only (but in *F. pusilla* abundantly) at respectively two sites in southern England and one site in north west England, always virtually confined to mines close to the ground.

In culture mines of *Heterartherus vagans* and *F. dohrnii* (both *Alnus glutinosa*), *H. microcephalus* (Klug) (on *Salix aurita*), *H. nemoratus* Fallén), *Profenusa thomsoni* (Konow), *Scolioneura betuleti* and *Messa nana* (all *betula*), *Profenusa pygmaea* (on *Quercus*) and *Fenella nigrita* (on *Potentilla reptans*) were all rejected; though some of the mines of *F. dohrnii*, and *Heterarthrus* on both *Alnus* and *Betula*, were probed. Females reared from both *F. pusilla* and *F. dohrnii* successfully attacked *F. pusilla*. The biology is essentially as in *X. lustrator*, except that the host is acceptable only when the mine is about half grown or under; the initial paralysis of the host is even less complete and shorter-lived; the subsequent feeding period by the host results in as much as 100% mine enlargement and lasts for c. 2 - 3 days before the host rather abruptly ceases activity; and no tendency to lay more than one egg per host was noted (although more than one host is often parasitized in multi-host confluent mines). The adult emerges in June/July and is long-lived: there seems to be only a partial second generation.

4. Genus ONCOPHANES Foerster

Oncophanes laevigatus (Ratzeburg) [= *lanceolator* (Nees); it is probable that *laevigatus* is also identical with the type species, *minutus* (Wesmael)].

A widespread and, especially in the south of Britain, abundant gregarious parasitoid of middle and late instar leaf-rolling Tortricidae and other small lepidopterous caterpillars of similar habits. Reared from many arboreal tortricids (unidentified species on *Prunus*, *Crataegus*, *Sorbus*, *Malus*, *Betula* and *Ulmus*), and also *Agonopterix nervosa* (Haworth) (*Oecophoridae*) on *Ulex europaeus*; and once each from the following Lepidoptera which are beyond its normal host range but include evidence that hosts are also sought in the field layer: *Scrobipalpa acuminatella* (Sircom) (Gelechiidae) on *Cirsium palustre*, *Prochoreutis sehestediana* (Fabricius) (Choreutidae) on *Scutellaria galericulata*, and *Phyllonorycter* sp. on *Salix aurita*. The usual hosts are mobile, in the sense of periodically constructing new retreats from which feeding sorties may be made, and mostly pupate among the leaves of their foodplant. *O. laevigatus* first emerges in May and is plurivoltine: it probably attacks different host species at different times of year, as many tortricids are univoltine.

In culture *O. laevigatus* has attacked all the species of Tortricidae in rolled, folded or spun leaves that have been offered [unidentified species on *Populus alba*, *Hypericum perforatum* and *Malus sylvestris*, and *Epinotia immundana* (Fischer von Röslerstamm) on *Alnus glutinosa*]. The host is stung through the leaf, and is permanently paralyzed. The parasitoid then enters the leaf-roll (etc.) and remains inside by the host, on which it host-feeds, for up to 1 day before re-emerging: oviposition occurs towards or at the end of this period. The eggs are slenderer and more curved than in the genera already discussed, and are arranged more or less precisely along the (sub) ventral aspect of intersegmental membranes, between several usually fairly central adjacent segments of the host's body. The eggs are somewhat sticky, but not firmly glued, and are easily removed. The host remains alive (for up to 10 days in the absence of parasitoid eggs), pulsating slowly, but has no gross mobility. The spindle-shaped papery cocoons are spun as an adpressed mass in the host retreat, usually flattened to the leaf surface(s). Brood sizes of c. 4 - 15 are most usual, and the adults remain loosely associated with their cocoons for a time after emerging, indicating that sib-mating may be habitual.

5. Genus RHYSIPOLIS Foerster

Rhysipolis decorator (Haliday)

In Britain a widespread and common parasitoid of *Caloptilia alchimiella* (Scopoli) (Lep.: Gracillariidae) and *C. robustella* Jäckh on *Quercus* in autumn, also attacking *C. betulicola* (Hering) on *Betula* especially earlier in the year. A very few male specimens have also been reared from confirmed *Phyllonorycter* mines on *Quercus* and *Betula* in the course of very intensive sampling (Askew and Shaw 1974, 1979; Shaw and Askey 1976), but these small species are outside the host range. One female reared from the poorly sampled *Acrocercops brongniardella* (Fabricius) (Gracillariidae) on *Quercus* may indicate an important, if local, midsummer host. *R. decorator* is bivoltine, first emerging at the end of May. Closely related and biologically similar forms attacking (a) *C. elongella* (L.) on *Alnus* and probably also *C. betulicola* on *Betula*, (b) *C. rufipennella* (Hübner) on *Acer pseudoplatanus* (in the Netherlands and Switzerland, but not so far found in Britain), and (c) *Parornix* (Gracillariidae) species on *Prunus* and perhaps *Crataegus*, are probably each distinct species. The usual hosts of *R. decorator* make a single small mine in their early instars, later feeding and moulting inside a series of two to three conical folds, constructed usually on successive leaves; and the substantial cocoon is spun on the lower surface of the leaf usually some distance away from the final cone. The host is attacked in its final cone, rarely its penultimate cone, as either a penultimate or more often final instar larva.

Experimental sleevings of *R. decorator* from *C. alchimiella* with *Phyllonorycter quercifoliella* (Zeller) on *Quercus robur* led to neither parasitization nor host-feeding. *Caloptilia syringella* (Fabricius) in *Syringa* rolls was similarly rejected. Adults from *C. alchimiella* readily parasitized *C. robustella* in sleeves and *C. betulicola* in tubes, infrequently host-feeding. The adult parasitoid patrols the cone, repeatedly making rapid thrusts with its ovipositor through the leaf and into the cavity, by which means it eventually stings the host and withdraws its ovipositor. The venom causes temporary paralysis, and oviposition takes place from outside the cone. The elongate and strongly curved egg is placed snugly and accurately along an intersegmental membrane, usually between abdominal segments. It is glued so strongly that it cannot be detached without damage. Superparasitism is frequent - even usual - both in the field and in culture, and appears to take place during a single visit, but only one parasitoid cocoon per host ever results. Within about an hour the host recovers full mobility and continues to feed; however, at the end of the feeding period of that instar, whether it is nominally penultimate or final, the host spins a cocoon inside its cone (in an experimental sleeve of *C. robustella* a few of the parasitized hosts made cocoons outside their cones, as is normal, but in all other cultures and in the wild the cocoon appears to be almost invariably constructed in the cone attacked by *R. decorator*), inside which its development is arrested in prepupal proecdysis. The parasitoid egg sometimes hatches before the host spins its cocoon; in either case, the first instar larva does not fully emerge, its caudal half remaining within the somewhat horny eggshell (which collapses only posteriorly) during the early part of its feeding, and it only fully quits the eggshell in a later instar after the host has become moribund in its cocoon. Despite its proximity to the host's body at all times, the head of the first instar larva bears antennae comparable with those of other Exothecini. *R. decorator* makes its own cocoon, in appearance very similar to that of a solitary *Oncophanes*, within that of its host.

Rhysipolis hariolator (Haliday)

Widespread and locally common in Britain as a parasitoid of *Parornix betulae* (Stainton) on *Betula* and *P. devoniella* (Stainton) on *Corylus avellana*. Previous records from *Phyllonorycter* species on *Corylus* (Shaw and Askew 1976) may have been in error: the mine and fold of *P. devoniella* each closely resemble mines of this genus. The host larva makes a tentiform mine which it leaves in its final instar to make one or more folds at this or another leaf edge, in which it completes its feeding. Pupation takes place in a small tight fold at the edge of a different leaf, either of the foodplant or beneath it. Both of these hosts are bivoltine in southern Britain where *R. hariolator* is also bivoltine and well synchronized, first emerging in May/ June.

The host is attacked as a final instar larva, perhaps exclusively so, in both the mine and the fold: hosts attacked in the mine proceed to a folding stage. Egg placement and the tendency to superparasitism are as described for *R. decorator*, and similarly the host resumes feeding after initial paralysis only to die in its cocoon which is, however, usually spun in its normal situation away from the last fold.

Rhysipolis ?meditator (Haliday) (type-species)

Widespread and abundant in Britain as a parasitoid of *Mompha raschkiella* (Zeller) (Lep.: Momphidae) mining *Chamaenerion angustifolium*; a single rearing from *M. terminella* (Humphreys and Westwood) mining *Circaea lutetiana* suggests that a wider range of leaf-mining Momphidae may be used, but only *M. raschkiella* has been adequately sampled. The latter makes blotch mines and is able to change leaves, probably usually doing so at least once or twice before it is fully fed. It pupates in a cocoon spun in debris or a tightly folded leaf near the ground, and is largely bivoltine. *R. ?meditator* is well synchronized and similarly chiefly bivoltine, first emerging in June.

The host is attacked as a final instar larva, possibly exclusively so. Egg placement and the tendency towards superparasitism are as described for *R. decorator*. The host dies in prepupal arrest in its cocoon, which is almost invariably spun in its usual situation, inside which the parasitoid makes its own cocoon. Eggs of the parasitoid have not been found to hatch before host cocoon formation and preliminary observations suggest that, within the attacked instar, feeding by parasitized larvae (which is certainly resumed) may be curtailed compared with unparasitized individuals. Although any such tendency was not noted in *R. decorator* or *R. hariolator*, this requires further investigation in all three species.

Rhysipolis, spp. indet.

Two as yet unidentified, and biologically uninvestigated, species have been reared from cocoons of (a) *Phyllonorycter emberizaepenella* (Bouche) mining *Lonicera periclymenum* (Netherlands, not so far in Britain) and (b) *Phyllonorycter ? schreberella* (Fabricius) mining *Ulmus* (Switzerland, not so far in Britain). It is of considerable significance that these two hosts differ from most *Phyllonorycter* species in constructing strong cocoons in the mine (which are further protected by being only feebly connected to the leaf tissue), no doubt aiding overwintering in the face of the abnormal susceptibility of these leaves to fungal decomposition.

Tribe ROGADINI

1. Genus CLINOCENTRUS Haliday

Clinocentrus gracilipes (Thomson)

In Britain a widespread and abundant parasitoid of all sampled Choreutidae (Lep.) in low vegetation: *Prochoreutis sehestediana* and *P. myllerana* (Fabricius) on *Scutellaria galericulata*, and *Anthophila fabriciana* (L.) on *Urtica*. *Prochoreutis* species have two summer generations, at least in southern Britain, larvae appearing in June/July and again in July/August. The larval stage almost certainly does not overwinter, though the life-histories of these two moths are incompletely known. *A. fabriciana* overwinters as an early larval stage (Shaw 1981a) and is fully grown by June after four larval instars: subsequently there are one to two further summer generations. Both *Prochoreutis* and *Anthophila* spin webs on leaves of their foodplants, causing them to form boat-like concavities or open pods, in which the larva rests and feeds in semi-concealment. About two or three leaf changes are usual during the larval life; and subsequently a dense, silken double cocoon is constructed amongst debris on the ground or in a more or less folded leaf, usually below and well-distanced from the feeding site. *C. gracilipes* is largely bivoltine and overwinters as a prepupa inside the "mummified" host prepupa in its cocoon, from which it first emerges in mid to late June. Synchronization of *C. gracilipes* with its ubiquitous host, *A. fabriciana*, on which it is usually locally entirely dependent, is very poor as the overwintering host generation is almost completely missed. As a parasitoid of *Prochoreutis* it is far better synchronized, but *Prochoreutis* species are extremely local, occurring chiefly in fens, and support only a minute fraction of the British population of *C. gracilipes*.

In culture *C. gracilipes* readily and successfully attacks *Choreutis pariana* (Clerck) (Choreutidae), which feeds on rosaceous trees in a similar way, but it has never been reared from extensive collections of this arboreal host (e.g., Shaw, in press and unpublished) even at sites where it was causing heavy mortality to *A. fabriciana* on *Urtica* beneath the trees. Various tortricid and yponomeutid larvae of apparently similar habits were consistently rejected. *A. fabriciana* was used for detailed experimental rearings, using parasitoids reared from both *Prochoreutis* and *Anthophila*. Third and fourth (= final) instar larvae in their webs are accepted, sometimes even if subactive in proecdysis, but naked hosts are consistently ignored. The adult probes the host web with its ovipositor apparently at random (and indeed it makes lengthy searches of recently vacated webs) and from many angles, periodically making sharp stabbing thrusts, and rapidly withdraws the ovipositor after eventually stinging the host. The venom rapidly causes temporary paralysis, during which the adult parasitoid relocates the host and oviposits through the web and into its body. Host-feeding has never been seen to take place, and nor is there a tendency towards superparasitism at a single visit. The egg is laid in a transverse position immediately beneath the epidermis, to which it adheres, and is clearly visible externally. Except that the egg occupies a central position in a body segment and is placed below the skin, egg placement is remarkably similar to that of *Rhysipolis*, and the following effects of the venom (Shaw 1981b) are identical: after temporary paralysis the host recovers mobility and feeding activity (seemingly undiminished, but precise data lacking) and, at the end of the feeding period of whichever instar is attacked, it is switched to a prepupal state in which it exhibits full cocoon-making behavior before eventually dying as a pharate pupa in developmental arrest, the body contents having undergone considerable histolysis. The parasitoid egg often hatches before the host becomes arrested but the bulk of larval development takes place afterwards, and the fully grown parasitoid larva forms its cocoon within the skin of the host. This "mummy" is a dark, hardened and uncontracted structure comprising the host larval skin fairly substantially lined with silk, and the adult parasitoid emerges from it by biting a hole just behind the hosts's head but not at any particular dorsoventral orientation. At the time of mummification a small quantity of fluid sometimes escapes as seepage near the caudal end of the host, but the mummy does not become glued down in any way.

C. gracilipes shares with all investigated Exothecini the following features: (a) it attacks only concealed or semi-concealed late instar hosts in situ; (b) it has a lethal venom controlling subsequent host behavior and development, which is applied as a separate action before oviposition; (c) it has rapid larval development upon a moribund and physiologically static host; (d) it is able to respond to the size of the host attacked by laying female eggs predominently in the larger host individuals and male eggs mainly in the smaller ones; (e) it invests a considerable period of time in each oviposition sequence; and (f) it overwinters as a prepupa in its cocoon.

Remarkably little is known of the host associations of other species of *Clinocentrus*, but probably "microlepidoptera" living in or under webs or in other spun retreats, but perhaps pupating elsewhere, will be the normal hosts. I have seen reared specimens of *C. excubitor* Haliday from Tortricidae and *C. vestigator* Haliday from *Ypsolopha vittella* (L.) (Yponomeutidae), and it is possibly significant that leaf-mining occurs in both of these lepidopterous families (admittedly mainly in early instars in the case of Tortricidae), and also in some (non-British) Choreutidae.

2. Genus **PELECYSTOMA** Wesmael

No species of *Pelecystoma* has been reared by me, but details given by Smith *et al.* (1955) for the Nearctic *P. harrisinae* (Ashmead) suggest that it occupies a biologically intermediate position between the otherwise widely spaced genera *Clinocentrus* and *Aleiodes*/*Rogas*. Rearing records given by Shenefelt (1975), including those for the type species *P. luteum* (Nees) and the gregarious (see Watanabe 1962) *P. tricolor* Wesmael from the Palearctic, suggest that *Pelecystoma* attacks fully exposed larvae belonging to "primitive" families of Lepidoptera (Limacodidae and Zygaenidae), which might suggest that this genus arose through an early response to the appearance of the naked feeding habit in Lepidoptera.

3, 4. Genera **ALEIODES** Wesmael and **ROGAS** Nees

As discussed by Shenefelt (1969), the correct application of generic names in this group is problematical: here they are applied sensu Shenefelt (1975) and, as no significant overall difference between the biologies of *Aleiodes* and *Rogas* has been evident from the fairly numerous species that I have studied, the two genera are treated together. However, there is undoubtedly a broader total host spectrum and more apomorphy in terms of life-history adaptations (in particular regarding overwintering) seen in *Aleiodes* than in *Rogas*. The latter genus seems to be chiefly univoltine and associated with Noctuidae.

In general, both genera (a) attack early instars of exposed "macrolepidoptera" (Hesperoidea, Papilionoidea, Bombycoidea, Geometroidea, Sphingoidea, notodontoidea and Noctuoidea in Britain); (b) exhibit various degrees of host specificity, voltinism and overwintering habits; (c) attack hosts away from foodplant substrates as readily as on them; (d) employ venoms that cause short-lived temporary paralysis as a handling device facilitating subsequent oviposition, but having no other detectable physiological effect on the host; (e) oviposit loosely into the host haemocoel as a separate action distinct from injecting venom; (f) kill the host in a middle instar, i.e., parasitized, making a somewhat contracted mummy; and (h) host-feed non-destructively and only when deprived of other nutritive moisture. Some illustrations of, and exceptions to, these generalizations are given below:

(a) In addition, *A. bicolor* (Spinola) is a regular parasitoid of *Zygaena filipendulae* (L.) (Zygaenidae) in which it overwinters but, as it also attacks *Polyommatus icarus* (Rottemburg) (Lycaenidae) on the same plant (*Lotus*) in summer, the use of *Zygaena* may be a secondary adaptation.

In experiments with *A. ?circumscriptus* (Nees) and *Orthosia stabilis* (Denis and Schiffermuller) (Noctuidae) it was found that mid-first, mid-second and early third instar hosts were approached with similar enthusiasm, but that first instar hosts were attacked only with difficulty and a significantly higher proportion of them did not survive the oviposition sequence itself. Development time to host mummification was shortest in third instar hosts (0 - 1 months) and longest by far in first instars (2 - 3 months). Mean handling time (i.e., the whole oviposition sequence) was shorter in second instars than in either first or third instars but the range was too great to assess significance. Encapsulation was significantly higher in third instar hosts than in firsts and seconds. The sex-ratio of adults reared from the three instars did not differ significantly although rather larger individuals resulted from the later instar hosts. Less detailed experiments with *A. geniculator* (Nees) parasitizing *Orgyia antigua* (L.) (Lymantriidae) and *Spilosoma* (Arctiidae) species indicated similar trends, as did experiments involving *R. rugulosus* (Nees) as a parasitoid of *Acronicta rumicis* (L.) (Noctuidae).

Table 1 - Host associations of some *Aleiodes* and *Rogas* species

Parasitoid	Host range (1 = overwintering generation, 2 = summer, if host ranges differ)	Voltinism	Overwinters
A.?circumscriptus	1. Grass-feeding noctuids (e.g. *Xestia*) 2. Arboreal noctuids (e.g. *Orthosia*, *Conistra*)	2	In host
A.?nigriceps	Low-feeding noctuids (e.g. 1. *Noctua*, *Xestia*, *Mythimna*; 2. *Phlogophora*, *Cucullia*)	2	In host
A.nigricornis Wesmael	Low-feeding/hiding noctuids (e.g. 1. *Apamea*, *Polia*; 2. *Orthosia gothica* (L.))	2	In host
A.pallidator	*Leucoma salicis* (L.)(Lymantriidae) only	1	In host
A.testaceus	Arboreal geometrids (e.g. *Operophtera*, *Colotois*, *Lomaspilis*)	2	As adult
A.modestus	Low-feeding *Eupithecia* (Geometridae)	1	As mummy
A.heterogaster	Arboreal notodontids (e.g. *Pheosia*, *Notodonta*)	1	As mummy
A.geniculator	Low-feeding lymantriids, arctiids and lasiocampids	2	In host
A.praetor	Arboreal sphingids	1	As mummy
R.grandis	Arboreal *Amphipyra* (Noctuidae)	1	As mummy
R.pulchripes (Wesmael)	Arboreal *Acronicta* (Noctuidae)	1	As mummy
R.rugulosus	Low-feeding *Acronicta*	1	As mummy
R.unipunctator (Thunberg)	*Apamea unanimis* (Hübner)(Noctuidae) ?only	1	As mummy
R.dimidiatus	Noctuids at ground level (e.g. *Cerapteryx*, *Agrotis*, *Caradrina*)	1	As mummy, or in host (*Caradrina*)

(b) Life-history data of some species for which I have most experience are summarized in Table 1. The habit of using host species in which the parasitoid is able to overwinter as an early instar larva in a living caterpillar is best developed in *Aleiodes*, although it is also seen in certain *Rogas* species not treated in detail here. Overwintering prepupae in mummies suffer high rates of predation and parasitism, and it is probably significant that the species listed in Table 1 that overwinter as mummies are on the whole far less abundant than those that do not.

It was found that, as in many other parasitoids, there is in almost all cases a very strongly defined division into arboreal species, and those on low vegetation. Thus the host ranges comprise groups of hosts in one or other of these partitions of the environment, closely related species from other niches being completely free of the parasitoid in nature. These "hosts" are, however, often attacked if offered in culture, especially after repeated or prolonged contact, but parasitoid survival is extremely poor. This probably reflects a lack of the regular contact that might lead to adaptation, but it also shows that if a physically acceptable potential host newly arrives in the parasitoid's searching environment it will be attacked and, if this happens frequently enough, it will presumably generate sufficient selection pressure to result in compatibility and hence an adoption of that host into the host range. Although rather limited in this context of host range extension, this does suggest ways in which resource abundance might indeed trigger behavioral responses relevant to the hypotehsis that the availability of behaviorally novel host groups has been an important evolutionary influence on the Rogadinae as a whole.

Noteworthy details for particular *Aleiodes* species are: (i) the exceptional and rigid seasonal alternation between arboreal and field layer hosts by *A. ?circumscriptus*, probably first arising as a response to seasonality in resource abundance; (ii) the thelytoky, probably associated with extreme host specificity, of *A. pallidator* (Thunberg); and (iii) the overwintering as an adult by *A. testaceus* (Spinola), enabling it to attack the very early spring larvae of arboreal geometrids soon after they hatch from their overwintering eggs.

(c) Both *Aleiodes* and *Rogas* species show moderate interest in host traces of various kinds (feces, silk, chewed leaves), but hosts are often first found visually (notably in *A. geniculator* and *R. rugulosus*) or by random antennal contact, and all species tested accepted isolated hosts freshly placed in glass tubes. Direct antennation of the host, and frequently also contact with the fore and/or mid tarsi, is important in the host acceptance process. The paralyzing sting (but see below) is brief, after which the ovipositor is withdrawn, and both the anterior legs and the antennae are used to manipulate and hold the host in position during the rest of the oviposition sequence. The adult parasitoid waits (c. 40 - 60 sec) until after paralysis has taken effect (c. 5 - 15 sec) before again inserting the ovipositor, usually only once, for oviposition (c. 30 - 80 sec). After oviposition the parasitoid usually remains standing over the host (c. 20 - 100 sec), sometimes antennating it; this might possibly be interpreted as guarding the host or keeping it associated with its substrate until the effects of paralysis start to wear off, although the adult parasitoid had usually left the host rather well before any such recovery (c. 2 - 5 min) was evident to me.

(d) All species studied, except for *A. heterogaster* Wesmael and *A. praetor* (Reinhard), use a venom to induce temporary paralysis. The lack of paralysis by these two species is probably an adaptation allowing their often monophagous arboreal hosts to continue to cling on to the foodplant while oviposition takes place. All other species studied (including those that are arboreal) insert the ovipositor twice - once to inject venom, then again to oviposit - and, by switching host individuals at the appropriate time in the oviposition sequence, oviposition into hosts that had not received venom could be induced: in these cases (*A. ?circumscriptus*, *A. ?nigriceps* Wesmael, *A. geniculator*, and *R. rugulosus*) parasitoid development was absolutely normal with no evident increase in encapsulation levels. Similarly, if stung hosts were removed before oviposition took place their development was completely normal and lead to healthy pupae whose formation lagged behind controls by only a few hours, probably representing no more than the full recovery time following paralysis [this was confirmed on a small scale for many species of both genera; in detail for *A. ?circumscriptus*, *A. modestus* (Reinhard) and *R. grandis* (Giraud)].

(e) Egg placement appears to be at random into the host's haemocoel in all species studied. However, the process of actual oviposition is prolonged enough to suggest that some tissue discrimination, at least, may occur: it is, of course, also possible that this prolongation might indicate that some further glandular secretion (e.g., for egg protection) is injected along with the egg at this, rather than the previous, insertion of the ovipositor. If this were to be the case, however, any gross controlling effect by the venom on host development could still be ruled out, as hosts that successfully encapsulated their parasitoids have all developed normally.

Provided they are active, parasitized hosts are accepted for oviposition without discrimination: subactive hosts, including those recently paralyzed, are avoided but otherwise post-oviposition displacement activity by the female parasitoid appears to be the only behavior tending to reduce superparasitism. No positive tendency to superparasitize a host at a single visit was seen except possibly in *A. heterogaster*.

(f) The presence of a parasitoid larva in the host retards its growth and prolongs the period spent in each instar, so that roughly half grown parasitized hosts are often mummified at about the time that unparasitized siblings pupate. The host instar killed, which within a particular association depends to some extent on the instar attacked, does not differ uniformly in the two genera, slightly abnormal lateness in some *Rogas* species (e.g., *R. dimidiatus* (Spinola) and *R. grandis*) being offset by extreme lateness in *Aleiodes modestus* which kills its very small host species as prepupae. Mummy structure is rather variable but usually involves some contraction of host segments at either the head or caudal end, or both, and the mummy is usually glued onto its substrate via a ventral opening in the thoracic region: this opening is made even by some species (e.g., *A. modestus*, *A. pallidator*) in which the mummy does not become glued down. *A. heterogaster* is a notable anomaly as it produces an inflated structure that is partly an air sac, from only the caudal half of the host. This is possibly an adaptation to the wetland habitats in which *A. heterogaster* often occurs, as the mummy is not glued down to the substrate, and floats in water. The quantity of silk spun as a lining in the mummy is variable, probably reflecting little more than the length of time spent in the mummy, and shows no consistent generic difference. The most silk-free mummies, however, are seen in *Aleiodes*.

(g) Emergence from the caudal end of the mummy is the rule for all the *Aleiodes* and *Rogas* species studied, individual exceptions being rare in both genera. This contrasts with *Clinocentrus* in which all mummies I have seen (*C. excubitor* as well as *C. gracilipes*) have emerged from the head end.

(h) Host-feeding is very rarely seen, and is always non-destructive. It usually involves rather large host individuals, after oviposition. Some species have also fed occasionally on the host's oral secretions that often appear as it is paralyzed. In general, however, honey:water is adequate for egg maturation and well-fed individuals do not host-feed.

5. Genus **PETALODES** Wesmael

Petalodes unicolor Wesmael (type-species)

A widespread, but extremely local, species in Britain, reared from larvae of the following Lepidoptera: *Hydriomena furcata* (Thunberg) (Geometridae) on *Salix* and *Corylus avellana*, and *Clostera pigra* (Hufnagel) (Notodontidae) on Salix. As larvae both hosts rest and feed beteen spun leaves: *H. furcata* is univoltine and overwinters as an egg, being available as a young larva early in spring; while *C. pigra* is more variable in its time of appearance but feeds later in the summer and overwinters as a pupa. *P. unicolor* is crepuscular and bivoltine, overwintering as an adult to oviposit in early spring (an adaptation also seen in *A. testaceus*) and appearing again in July and then late August/September (before hibernation). The host range is probably a good deal wider than that noted above: certainly *C. pigra* appeared to be absent from two sites at which *H. furcata* supported *P. unicolor* implying that different summer hosts would be involved. Undoubtedly all hosts, however, would feed in spun leaf packages or similar structures, and would probably be arboreal.

P. unicolor has been reared for several generations as a culture alternating between *H. furcata* and *C. pigra*. The following notes apply to parasitism of the latter host. No interest whatsoever was shown for naked hosts, but the host retreat (including feces and silk) elicited excitement whether or not it was tenanted. After an external examination of the host retreat with its short antennae, the parasitoid thrusts the whole of its abdomen (which in the female sex is laterally compressed, blade-like and considerably extensile) through the silk or into the leaf package, twisting it up to 90° in pursuit of the host if it is between leaves or in narrow runs. When contacted, the host is stung: temporary paralysis is rapid and the parasitoid quickly relocates the host, again using its abdomen alone, and reinserts its ovipositor. Oviposition itself takes about 90 - 250 sec, longer than in *Aleiodes*/*Rogas*, and the egg is placed in the haemocoel but fastened by its narrow end to abdominal muscle tissue. Unfortunately the effect of the venom alone has not been properly investigated, but nothing has suggested that it differs from that of *Aleiodes*/*Rogas*. As in a few species of *Aleiodes*, the mummy is not glued down although seepage occurs through a ventral thoracic opening, and it contains virtually no silk. Emergence is as in *Aleiodes/Rogas*. Although biologically rather close to *Aleiodes/Rogas*, *P. unicolor* differs in attacking only concealed hosts, and also in its ill-understood egg placement behavior. Its aberrant morphology is readily understood in terms of the hosts attacked, and it is of interest that *Petaloides*, probably having evolved from an *Aleiodes*-like ancestor using naked hosts, retains a fairly short ovipositor in its specialization on concealed hosts.

DISCUSSION

The above account is limited to the biology of some British Rogadinae and omits not only morphological data but also any information at all on very many genera (and even tribes) of World Rogadinae. It cannot, therefore, be seen as the basis for a rigorous phylogenetic study. The present hypothesis is a great deal more simple: that the biological adaptations described above, or very similar trends, led to particular conditions that provoked a transition from ectoparasitism to endoparasitism in cettain Rogadinae. The emphasis is on the kinds of interaction between host biology and parasitoid biology that actually occur, and it is not intended to imply that the species studied are themselves close to any sort of transition: extant species represent metastable states of biological efficiency and may be far distant from one another in evolutionary terms, being survivors of processes that have perhaps involved powerful selection pressures, and much extinction of transient forms in the face of competitive inefficiency or some other effective resource contraction. This is bound to be the case if behavioral aberrations, at first intrinsically inefficient but highly compensated by the advent in a changing environment of large and initially underexploited resources, precede physiological and morphological adaptations in the evolutionary process. Although direct evidence is admittedly lacking, there are reasonable grounds to suppose that there has been some sort of progressive evolution in the Rogadinae such that, for example, the extant genera *Colastes*, *Rhysipolis*, *Clinocentrus* and *Aleiodes*, which utilize progressively more "advanced" host groups, can be seen as illustrating a sequence of development in the exploitation of new opportunities. However, our knowledge of how the relevant host groups coevolved with their own resources, or how this incompletely understood host phylogeny has been distributed in terms of space, time and relative abundance, is so hazy that it is impossible to do more than merely speculate on tendencies. Thus, while the following summary (written in somewhat teleological terms for the sake of brevity) indicates how this may have happened as a result of exploiting hosts efficiently, and suggests some particular specializations that may have been important, it must be taken in the spirit of a speculative suggestion rather than as wild dogmatic claim.

The genus *Colastes* attacks the least "advanced" of the lepidopterous hosts and in *C. braconius* contains the species with the broadest host range of any of the Rogadinae studied, although this species has a long ovipositor and clearly specializes on fully grown hosts that live and pupate in their single mines (a habit that seems to encourage mine depth for protective isolation of the pupal stage). If the first instar parasitoid larva is mobile, precise egg placement is unimportant in a closed mine which is not about to be vacated by the host, and possibly an ancestral habit would have been simply to oviposit into the mine; however, better control is gained if the host is stung and immobilized, thereby preventing it from taking advantage of the maneuverability afforded by a deep mine to damage the ovipositor or the egg, and also preventing the host's subsequent pupation and hardening of its cuticle. The host's temporary recovery from paralysis, sufficient to defecate, is a further refinement, and its slow as opposed to outright death allows the young parasitoid to feed on fresh rather than putrid food.

The genera *Phanomeris* and *Xenarcha* appear to be specialized and probably rather recent responses to sawfly miners, which moult at the time of either leaving their flat mines to pupate elsewhere or else isolating themselves for pupation in small discs in the mine. The venom used by *Phanomeris* prevents the host from accomplishing this vital moult, thereby keeping it in its mine, and this leaves egg placement unimportant. However, there is some selection towards mines that are not fully grown, perhaps because the surprisingly agile hosts escape for longer in full-sized mines, which will often be already vacated in any case, and considerable time is invested in searching for a host within each mine visited. In *Xenarcha* this is more clearly seen, and the venom permits the host to recover considerable feeding activity and to grow in size, thereby providing a larger food resource, while retaining the advantages of attacking mines of a size most likely to contain relatively easily locatable hosts. The evident stickiness of the loosely laid egg is perhaps one way of ensuring that the first instar larva easily finds its food; mere oviposition precision being a useless strategy as the host subsequently moves away.

Oncophanes utilizes larger hosts than the other Exothecini studied and the tendency towards multiple oviposition is here successfully developed. Although some mine when young, when at the stage attacked its tortricid (etc.) hosts live in leaf-rolls (etc.) which are often partially open, and repeatedly spin fresh retreats for themselves, eventually pupating in situ. A paralyzing venom prevents host ecdysis or movement and ensures that parasitoid eggs are not sloughed at ecdysis or simply left behind; and eggs placed ventrally along host intersegmental membranes may be better hidden from small predatory invaders of the leaf-roll, and also help to ensure that the first instar parasitoid larvae easily find the host and do not wander right out of the roll. The tendency to use venoms that delay host death, providing a less putrid or even living food resource, is expressed in *Oncophanes* by use of a venom causing an even, long-term paralysis. (Gregarious development is known in some genera of endoparasitic Rogadini not studied by me, and it is possible that developments of the trend seen in *Oncophanes* - i.e., gregarious ectoparasitism of large hosts, involving precise egg placement and a controlling venom - may have preceded a transition to endoparasitism. The genera *Rhysipolis*, *Oncophanes* and *Clinocentrus* are morphologically close and, although the biologies of the studies species of *Rhysipolis* and *Clinocentrus* seem closest, there are vague literature records of gregarious development in some *Clinocentrus* species. There is, of course, no firm evidence that all endoparasitic Rogadinae, or even all species of the poorly studied genus *Clinocentrus* as accepted, comprise monophyletic groups. The view that the Rogadini arose from within the Exothecini leaves the latter as a paraphyletic group, irrespective of the possibility of the Rogadini being polyphyletic).

In *Rhysipolis* the primary specialization has been to take advantage of leaf-mining larval hosts which pupate in a strong cocoon capable of providing protection. By adapting to this situation, species of *Rhysipolis* have also been able to utilize hosts of high mobility - i.e., those which frequently change mines, or subsequently make leaf folds, independently of ecdysis - and its hosts may pupate completely away from their feeding site. The egg is firmly glued to the host integument, its alignment between body segments partly concealing it in a position that not only affords it protection as the host is exposed between mines or folds, but also prevents it from being scraped away against the small hole through which some of the hosts quit their feeding sites. The venom has several vital effects: firstly by causing temporary paralysis it enables eggs to be placed and attached with precision; secondly it permits the host to recover and to hide and feed until the end of its instar but then arrests it before ecdysis, thereby ensuring that the egg is not lost; and, most importantly, thirdly it switches the host to a prepupal phase so that, whichever host instar is attacked, cocoon formation still takes place. The parasitoid larva consumes the host in this arrested and protected state before spinning its own cocoon inside that of the host.

The kind of precisely predictable, and physiologically weakened, state of the arrested prepupal host of *Rhysipolis* is an important and provocative precursor to the advent of endoparasitism, with the added immediate advantage of better egg concealment and protection, and also possibly allowing host-derived nutrients to enter the egg through a hydropic chorion (unlike Exothecini, which lay well-yolked eggs, *Clinocentrus* does not host-feed). *Clinocentrus* uses a venom that has precisely the same effect as that of *Rhysipolis*, producing the same physiologically unchallenging and unvarying environment for its endoparasitic larva, and *Clinocentrus* even orientates the egg in a similar way that now seems to serve no clear purpose (though the behavior of the first instar larva is not known). The peripheral position of the egg, however, may be important in terms of oxygen availability as the host becomes physiologically inactive.

It is worth stressing here that there is little evolutionary opportunity for endoparasitism of tenthredinid sawflies to have arisen in the Rogadinae in the way that seems to have happened in association with lepidopterous hosts, because leaf-mining sawfly larvae undergo ecdysis immediately before cocoon construction (and usually before leaving the feeding site) which is always undertaken by a specialized non-feeding instar. Any venom, therefore, that switched a sawfly larva to a prepupal state would provoke an ecdysis before cocoon construction, which could only be survived by specialized (e.g., stalked and anchored, as in Tryphoninae) eggs of a kind not seen in Rogadinae. It might, however, be even more relevant that the leaf-mining habit is evidently a fairly recent apomorphous condition in sawflies, whereas it has much deeper roots in the Lepidoptera in which it is mostly found in relatively plesiomorphous groups. Similarly, any possible importance of dipterous hosts in the evoluation of the Rogadinae can be dismissed: Agromyzidae are included in the wide host range of *C. braconius*, but clearly leaf-mining is an extreme apomorphy in the Diptera, and the Agromyzidae a very recent family (Rohdendorf 1974: 305). In any case, the biology of Cyclorrhapha seems unconducive to extreme venom and egg placement specializations by ectoparasites. Leaf-mining in Coleoptera is also a generally apomorphous habit from which little further specialized behavior has developed, although some mining species move from one leaf to another and almost all pupate in the ground (Crowson 1981: 593). Indeed, as the behavior at metamorphosis of Coleoptera is broadly suitable, it would not be surprising to find some Rogadinae, perhaps related to *Phanomeris* or *Xenarcha*, specifically associated with phytophagous beetles - possibly even as endoparasites. However, the view that endoparasitism in the Rogadinae arose from an originally ectoparasitic stock attacking leaf-miners, and developed to the level seen in *Aleiodes*/*Rogas* in the course of adaptations to new opportunities as their host group as a whole evolved in behavior, can be applied only to lepidopterous hosts.

Adaptation to an endoparasitic way of life by *Clinocentrus* has depended heavily on the venom system of its ectoparasitic precursors, but endoparasitism was presumably also encouraged by the availability and exploitation of hosts which feed in less concealed sites than those of the ectoparasites, as the protection of the egg, for example against desiccation, would be partly ensured by the host's integument. Once established, however, endoparasitism raises very different demands from ectoparasitism if it is to be adapted successfully to fully exposed hosts. The ectoparasites tend to attack concealed, late instar hosts, and their protected progeny have high survival rates. Superparasitism is inherently low because of long handling times, low fecundity associated with large anhydropic eggs, and an ability to reject subactive hosts. On the other hand, endoparasites of fully mobile hosts would not so easily be able to avoid superparasitism and, furthermore, the first parasitoid larva present would soon come to control the host's body well enough to destroy any subsequent eggs. As hosts that feed exposed became available and were adapted to, they may well have attracted high levels of superparasitism, because of much reduced handling times and the higher fecundities associated with this and the scope for smaller, hydropic eggs. On this basis, natural selection would favor endoparasitism of the host earlier in its life, as the first endoparasite present would be at a competitive advantage, but for this to be taken very far the host would subsequently have to be able to grow and moult so that a sufficient food resource was eventually present. The controlling effect of a venom that prevented host ecdysis would no longer be advantageous, but its absence would provoke a further and power ful selection towards attacking younger hosts with less copious physiological defenses against foreign bodies, and also to specialize by evolving specific physiological tolerance towards narrow host ranges. (The striking difference between firstly *Clinocentrus gracilipes* and secondly apparently all *Aleiodes* and *Rogas* species in their abilities to develop in experimental hosts outside the host range - i.e., in this case species closely related to the natural hosts but living in a different environment in which the parasitoid does not usually search - is an illustration of this trend). The evolutionary distance between these two suits of biological characters, befitting successful ectoparasitism and the first establishment of endoparasitism on the one hand and successful endoparasitism of exposed hosts on the other, thus involves various selective influences made particularly harsh by being imposed in concert. This may account for the apparently large biological gap, perhaps partly filled by relict genera such as *Pelecystoma*, between *Clinocentrus* and the again successful genera *Aleiodes* and *Rogas*, by which the transition has been fully accomplished. In the latter two genera a throwback to an ectoparasitic ancestry in which a far greater role was played by the venom, now only a temporary handling device which is still useful under most (but not all) circumstances, is perhaps seen in the separate insertions of the ovipositor for paralysis and for subsequent oviposition. Killing the host before it is fully grown may also be indicative that *Aleiodes* and *Rogas* succeeded chiefly by a fairly rapid progression to attacking the host very early: some of the (unstudied) gregarious endoparasitic Rogadini, briefly mentioned above in connection with *Oncophanes*, might, of course, turn out to be merely extensions of the *Aleiodes/Rogas* form of development, taking advantage of this extra host capacity.

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REFERENCES

Achterberg, C. van. 1976. A preliminary key to the subfamilies of the Braconidae (Hymenoptera). Tijdschr. Ent. 119: 33-78.

Askew, R. R. and Shaw, M. R. 1974. An account of the Chalcidoidea (Hymenoptera) parasitizing leaf-mining insects of deciduous trees in Britain. Biol. J. Linn. Soc. 6: 289-335.

Askew, R. R. and Shaw, M. R. 1979. Mortality factors affecting the leaf-mining stages of *Phyllonorycter* (Lepidoptera: Gracillariidae) on oak and birch. 2. Biology of the parasite species. Zool. J. Linn. Soc. 67: 51-64.

Beirne, B. P. 1946. Notes on the biology of some hymenopterous parasites of the beech weevil (*Rhynchaenus fagi* L.) (Col.). Proc. Roy. Ent. Soc. London (A) 21: 7-11.

Crowson, R. S. 1981. The biology of the Coleoptera. Academic Press.

Rohdendorf, B. 1974. The historical development of Diptera. Univ. of Alberta Press.

Shaw, M. R. 1981a. Overwintering of *Anthophila fabriciana* (L.) (Lepidoptera: Choreutidae) in England, with notes on some of its parasites (Hymenoptera). Entomologist's Gaz. 32: 203-204.

Shaw, M. R. 1981b. Delayed inhibition of host development by the non-paralyzing venoms of parasitic wasps. J. Invert. Pathol. 37: 215-221.

Shaw, M. R. In press. Foodplants and parasites (Hymenoptera: Ichneumonoidea) of *Choreutis pariana* (Clerck) (Lepidoptera: Choreutidae) in Edinburgh. Entomologist's Gaz.

Shaw, M. R. and Askew, R. R. 1976. Ichneumonoidea (Hymenoptera) parasitic upon leaf-mining insects of the orders Lepidoptera, Hymenoptera and Coleoptera. Ecol. Ent. 1: 127-133.

Shenefelt, R. D. 1969. Notes on some Rogadine genera (Hymenoptera: Braconidae). Proc. Ent. Soc. Washington 71: 428-444.

Shenefelt, R. D. 1975. Hymenopterorum Catalogus 12: Braconidae 8, Exothecinae and Rogadinae. Dr. W. Junk.

Smith, O. J., Diboll, A. G. and Rosenberger, J. H. 1955. Laboratory studies of *Pelecystoma harrisinae* (Ashmead), an adventive Braconid parasite of the Western Grape Skeletonizer. Ann. Ent. Soc. Amer. 38: 232-237.

Watanabe, C. 1962. Occurrence of *Pelecystoma tricolor* Wesmael in Japan (Hymenoptera: Braconidae). Insecta Matsumurana 25: 41-43.